# CONTENTS

# INTRODUCTION

Seaweeds rarely get the affection they deserve. The Roman poet Horace wrote that "Without money, birth and virtue are more worthless than seaweed." A common English name for them is wracks, which comes from the same root as the word "wreck."

But seaweeds are not wrecks, nor worthless, washed-up things. They are astonishingly diverse, vibrant, and important. The soft fronds of jelly weeds are delicate enough to be eaten as noodles, while on the other side of the Pacific Ocean, their kelp relatives can grow as tall as the giant redwoods that they face along the length of the northwest coast of America. The seaweeds provide the foundations for coastal ecosystems from the tropics to the poles, they support sparkling worlds of animal and microbial biodiversity, and they are physically strong enough to absorb wave action and slow coastal erosion along shorelines the world over. They have provided food, fodder, and fertilizer to coastal communities for thousands of years and feed large swathes of island populations to this day.

We should not, however, take seaweeds for granted. The coastal communities that seaweeds support are moving out of balance as climate

change continues its bite and as humans gamely exploit, but inexpertly manage, ecosystems that are millions of years old. Increasing numbers of seaweed blooms are being reported in the Caribbean, the Yellow Sea, and the Atlantic, with beaches becoming ever more clogged as unprecedented quantities of biomass wash up on them. Our best models predict that these seaweed blooms will spread to the North Atlantic, the Mediterranean, and the shores of Africa and South America, all of which are beginning to see an increase in beach-cast weeds. The seaweeds are as integral to our shores as plants and trees are to dry land: if we want to understand the world around us, we need to recognize, respect, and appreciate their diversity.

**ABOVE** | Fronds of the red seaweed *Asparagopsis taxiformis* rise above the flatter, forked fronds of the brown seaweed *Dictyota dichotoma.*

# WHAT ARE SEAWEEDS?

Life on today's Earth is driven by photosynthesis. About half of that photosynthesis is carried out by an evolutionary group called the "land plants," which are our trees and grasses and flowers. The other half is carried out by an older, broader group of organisms called the algae. The algae are astonishingly diverse, but some of them are large and look plantlike and live in the sea, and these "macroalgae" are our seaweeds.

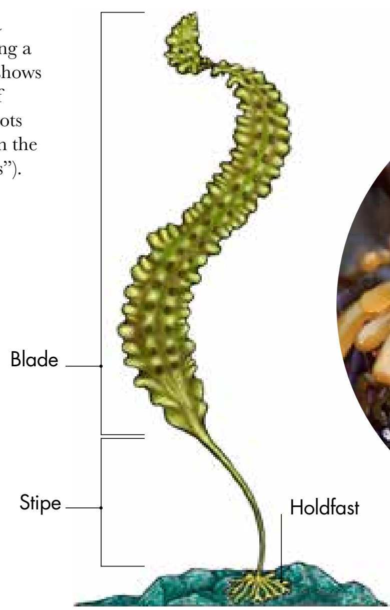
## THE PARTS OF SEAWEEDS

The body of a seaweed is called a frond or thallus: an ancient Greek word for a young plant shoot. In many seaweeds, this is divided into three distinct sections: the charmingly named holdfast, the stipe, and the blades. The holdfast tethers a seaweed to the rock or sand beneath it. Holdfasts take many shapes but usually look like large suckers or a tangled collection of roots. Not all seaweeds have holdfasts: some are free-floating, with the best known being the *Sargassum natans* and *Sargassum fluitans* that grow holdfast-free thousands of miles from any shoreline in the mid-Atlantic's Sargasso Sea.

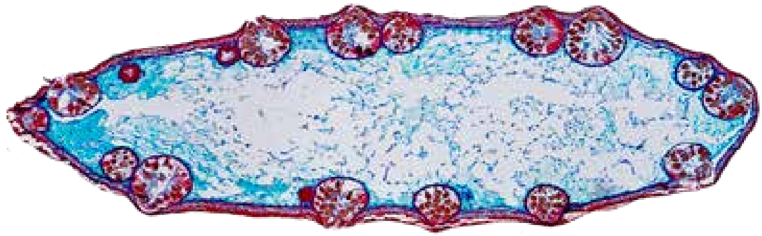
In larger, tethered seaweeds, the holdfast often develops into a prominent stalk, called the stipe, which connects the holdfast to the fleshier, leaflike body of the seaweed. This fleshy part is called the blade. Different blades may be leafy or straplike, or bushy and branched.

Botanically, a thallus is a structure that is relatively undifferentiated and seaweed thalli have simple internal architectures. Many species consist of only a couple of cell types, with larger species having slightly different outer and inner cell layers that can develop into visible structures such as air bladders. Some cells are able to divide continuously and these form a meristem—the growing core of each seaweed. When seaweeds become fertile, they develop organs that contain

**RIGHT** | The parts of a seaweed, illustrated using a brown kelp. The inset shows the tangled root type of holdfast (the tangled roots are called haptera, from the Greek for "attachments").




**RIGHT** | A cross section through a fertile tip (a receptacle) of the brown seaweed *Fucus*. This receptacle measures half an inch from left to right and the circles are structures called conceptacles, which make the reproductive cells.



reproductive cells and often appear as blisters on the thallus. Seaweed reproduction is complex so the names given to reproductive structures differ across different species.

By way of comparison, land plants are much more highly differentiated and can contain 50 or more cell types (humans have more than 200), arranged into organs that are connected by extensive vascular systems to allow nutrients from the soil to flow to the leaves and carbon from the air to flow to the roots.

Seaweeds absorb both their nutrients and their carbon from the same place: the water around them. Radioisotope work has shown that the spongelike architecture of some seaweed species does allow a degree of nutrient flow between the dividing meristem and the outer blade. This means that seaweeds have much less need of differentiated organs than plants do and mostly live without them.

**BELOW** | The green seaweed *Acetabularia major*. The umbrella-like caps are the fruiting bodies and only appear when this species becomes fertile, a little like mushroom caps.

# EARLY EVOLUTION

We said that the seaweeds were diverse; we will now discover how diverse. The land plants are drawn from one evolutionary group, a phylum called the Embryophyta. The seaweeds, on the other hand, come not from one evolutionary group, but at least three: the Rhodophyta, the Chlorophyta, and the Phaeophyceae. These are more commonly and respectively called the red, green, and brown seaweeds. Each forms either its own taxonomic phylum or, in the case of the Phaeophyceae, a smaller evolutionary group called a class. Why do we group such wildly different organisms together under the same word: seaweed? To answer that question, let us digress to consider how life on Earth has evolved.

## THE FIRST SINGLE-CELLED ORGANISMS

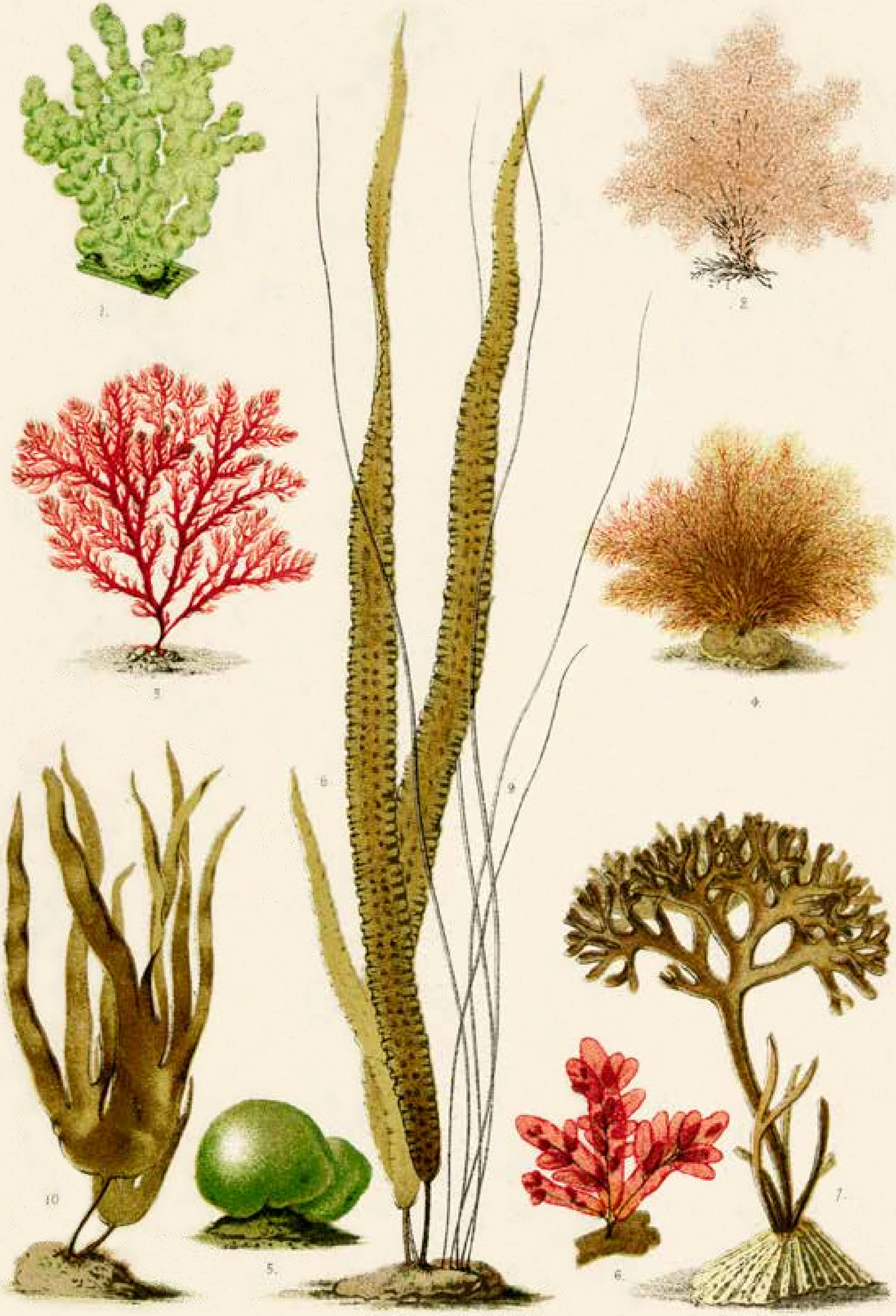
The Earth is around five billion years old, and life began a little under four billion years ago. A billion years is an almost incomprehensibly long time: anatomically modern humans are thought to have existed for around the past 200,000 years, which is a mere two hundredths of one percent (0.02 percent) of a billion years. To put that very small number into perspective, the last 12 months were roughly 0.02 percent of the time that has elapsed since the building of the Great Pyramid of Giza: a billion years is a very, very long time.

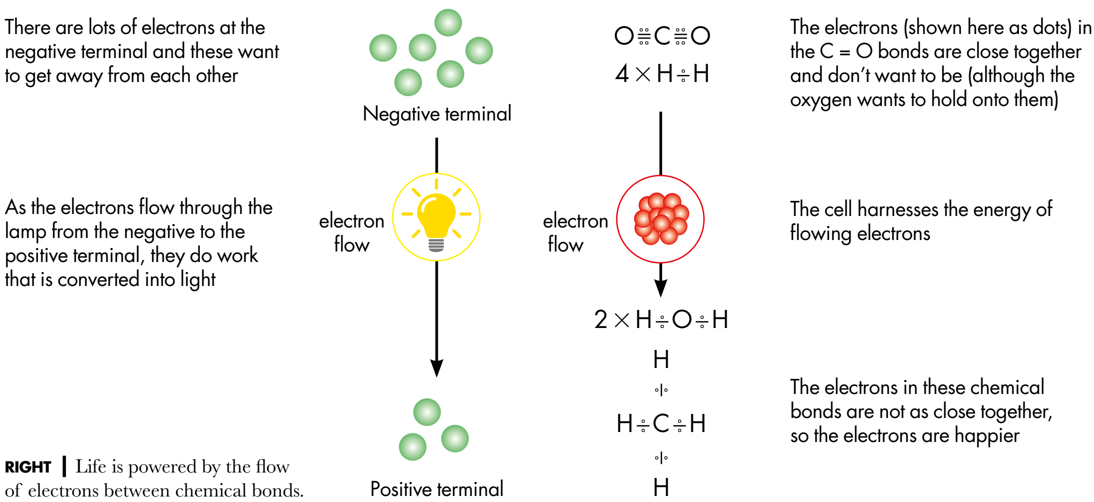
Nonetheless, five billion years ago, the early Earth solidified from a swirl of cooling stardust. As it cooled, water condensed, clouds formed, and it began to rain. It continued to rain for a billion years, pouring water into the oceans in which life began in the Archean eon, probably around 3.8 GYA (GYA = giga years ago = billion years ago). What form this early life took is much debated, but it would probably have comprised ribonucleic acid (RNA) polymers. Like DNA, RNA is a nucleic acid that can store information in its sequence, but RNA is more reactive than DNA so these early polymers could catalyze simple chemical reactions. Over time, these information-storing catalytic polymers became enclosed in protective membranes, giving the first single-celled organisms.

Where did this early life get its energy from? The simple answer is electricity. Electrical circuits work by gathering negatively charged electrons at one place (the negative terminal) and removing them from another place (the positive terminal). Like charges repel each other, so when the terminals are connected, electrons flow down the connecting wire from the negative terminal to the positive terminal. As the electrons move, their energy can be harnessed and put to useful work.

Living things generate electricity using a very similar trick. Electrons form the outer shells of atoms and when two atoms join together they do so by sharing their outer electrons in a chemical bond. The electrons in some bonds are forced together more closely than in others. The trick that early life discovered was to move electrons from electron-dense chemical bonds into less electron-dense bonds, harnessing the energy as the electrons flowed from one bond to the other.

**OPPOSITE** | An 1879 illustration from the Spanish periodical *El Mundo Ilustrado*. Nos. 2–4, 6, and 7 are red seaweeds, 8–10 are brown seaweeds, 1 is a green freshwater weed, and 5 is now known to be a bacterial colony.






**RIGHT** | Life is powered by the flow of electrons between chemical bonds.

For about a billion years life powered itself in this electrochemical fashion, prizing apart simple molecules, letting the electrons flow through its cells to power life's metabolism, and then handing the electrons back to new, less electron-dense bonds between the same atoms. For example, one group of early organisms, called methanogens (methane makers), harvested electrons from the bonds in carbon dioxide ($CO_2$) and hydrogen ($H_2$) and handed them back to the rearranged carbon, hydrogen, and oxygen atoms to make methane ($CH_4$) and water ($H_2O$). Early life proved very good at this simple electrochemistry, evolving into today's bacterial and archaeal lineages, which between them are capable of breaking down around a hundred different simple organic and inorganic chemicals. The microbes that live on sulfates in hot springs or on the hydrogen sulfide released by seafloor hydrothermal vents are both their literal and spiritual ancestors.

## THE GREAT OXIDATION EVENT

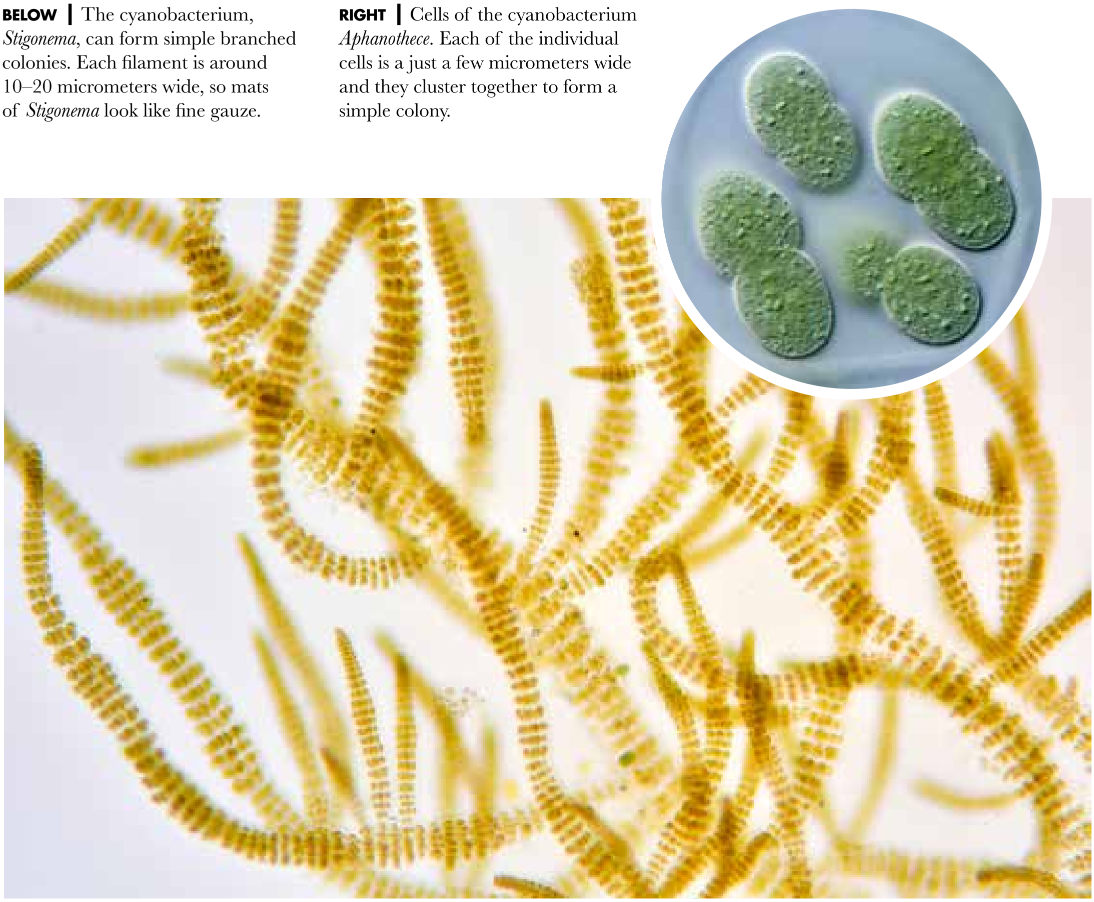
Although simple molecules were present in the early oceans, they were not abundant and early life lived on molecular scraps. All the while, it was sitting in a literal sea of unobtainable electrons. Water, $H_2O$, is an excellent source of electrons because its single oxygen atom forms electron-dense bonds with each of its two hydrogens. These electrons can drive relatively strong electrical currents if they can be prized away from oxygen's clutches.

Unfortunately, cracking open a water molecule to get at its electrons is a difficult trick because oxygen likes to hold on to those electrons. The metabolic breakthrough came eventually, around three billion years ago, with the evolution of photosynthesis by a group of organisms called the cyanobacteria (blue-green bacteria). Over many millions of years, the cyanobacteria evolved complex electron transfer chains: a sequence of reactions that allowed them to use the energy in sunlight as a crowbar. The cyanobacteria crowbarred water open, diverted its electrons through their electron transfer chains to power themselves, and then handed the exhausted electrons back to water's oxygen, creating and releasing oxygen gas. Photosynthesis was such a successful adaptation that cyanobacterial growth took off and began to reform the world, releasing so much oxygen that, slowly but surely, they changed Earth's atmosphere from a methane- and carbon-dioxide-rich one into the one that we have today, in which oxygen makes up around one-fifth of the air around us. This terraforming of the Earth's atmosphere by the cyanobacteria is now known as the Great Oxidation Event and we think it lasted from around 2.5 to 2 GYA, or around half Earth's lifetime ago.

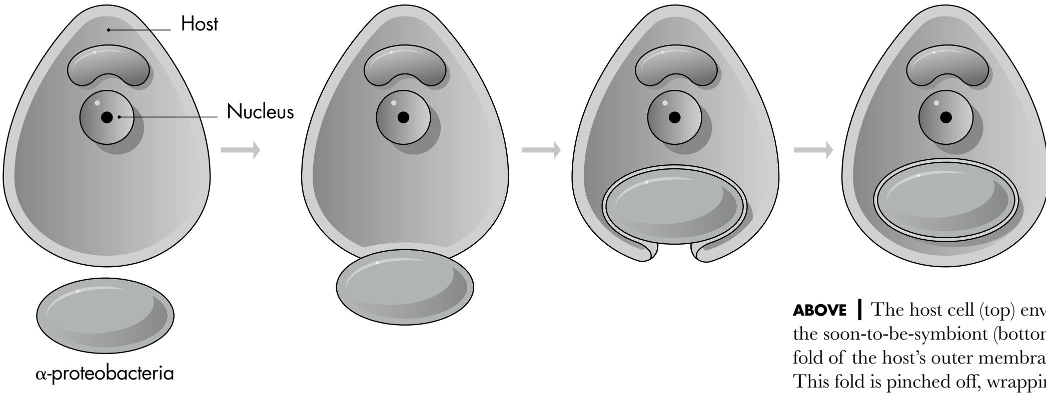
The cyanobacteria did not have it all their own way, however. Living things are engaged in a constant tussle for Earth's limited resources: when one species finds a new trick, others must find a way to adapt if they are not to be outcompeted. In the case of photosynthesis, the other bacterial species elegantly turned the cyanobacteria's own success against them by using the oxygen ($O_2$) gas that the cyanobacteria released. We have mentioned that oxygen strongly attracts electrons, which makes the $O_2$ molecule very reactive because it can pull electrons away from other molecules. This, incidentally, is why you need $O_2$ to burn things: a flame is simply the heat that results as oxygen very rapidly rips electrons away from the fuel. So, the trick that other microbes developed was to generate energy by burning simple compounds in the cyanobacterial-released $O_2$ and this metabolic riposte evolved into the process that we now call respiration.

**BELOW |** The cyanobacterium, *Stigonema*, can form simple branched colonies. Each filament is around 10–20 micrometers wide, so mats of *Stigonema* look like fine gauze.

**RIGHT |** Cells of the cyanobacterium *Aphanothece*. Each of the individual cells is a just a few micrometers wide and they cluster together to form a simple colony.



PRIMARY ENDOSYMBIOSIS




**ABOVE** | The host cell (top) envelops the soon-to-be-symbiont (bottom) in a fold of the host's outer membrane. This fold is pinched off, wrapping the symbiont in a double membrane.

## ENDOSYMBIOSIS

Respiration and photosynthesis are powerful weapons to have in one's armory when competing for limited resources, and other microbes soon wanted in. The exact details remain a matter for debate but, sometime between 1 and 2 GYA, a campaign of cellular piracy took place in which one group of organisms engulfed α-proteobacteria that were capable of respiration. However, instead of being digested, the engulfed α-proteobacteria survived inside their captors and established a symbiosis. Because one species is living inside, rather than alongside, the other, this is called an internal symbiosis or endosymbiosis. This was a "primary" endosymbiosis: one host engulfed something that had previously been free-living.

Slowly and gradually, the new endosymbiont adjusted to its surroundings: it kept both its own cell membrane and the membrane that its host had used to engulf it, leaving it wrapped in a characteristic double membrane. The host and endosymbiont began to synchronize their cells by moving a number of genes from the endosymbiont's DNA across to the host's DNA until, at last, they stopped being two separate organisms and became one single, compartmentalized cell. Other compartments followed and the host DNA became wrapped in a membrane of its own to form a distinctive cell organelle called the nucleus. The nucleus sitting inside the cell looks, through a light microscope, a little like the stone sitting inside a fruit—so much so that an early-twentieth-century biologist called the possessors of such organelles "true stoned" cells, or "eukaryotes" (Greek: *eu* = "true"; *karyon* = "stone or nut of a fruit"). Today, almost every creature we can see with our naked eye, including ourselves, is a eukaryote and our cells still contain the double-membraned organelles that were once α-proteobacteria. We now call those organelles mitochondria and they continue to respire using the same trick that bacteria developed over two billion years ago to compete with cyanobacteria.

The story of endosymbiosis all sounds extremely unlikely and, indeed, it is extremely unlikely. But a billion years is a very, very long time and, given long enough, unlikely things can and do happen. It is thought that, as with many long-lasting relationships, the establishment of this primary endosymbiosis did not happen overnight: instead, the host and symbiont would have learned first to live in association before the symbiont became attached, and then protected, and then, finally, enveloped.

## EUKARYOTIC ALGAE APPEAR

When endosymbiosis works, one lineage gains an entirely new set of abilities. There is no need to painstakingly build something from scratch because one can just steal a whole new metabolic pathway in one fell swoop. It is no surprise, then, that after acquiring mitochondria, some organisms tried the same trick again. Perhaps around 1 or 1.5 GYA, they engulfed and kept hold of cyanobacteria, creating a second organelle that became the chloroplast, in addition to the mitochondria that they already had. Again, this was a primary endosymbiosis in which the host cell engulfed and kept a previously free-living organism and this time it resulted in an organism that could both make food from light and then burn that food to power itself in the dark. These were the first eukaryotic algae: single-celled marine species that were probably a few tens of micrometers across and could make food from light or, in the jargon, were photoautotrophs (light-self-feeders).

These early microalgae (single-celled algae) contained chloroplasts that had been obtained from a primary endosymbiosis and they separated, perhaps between 1 and 1.5 GYA, into what we now know as the red and green lineages: the Rhodophyta and Chlorophyta, respectively (the Phaeophyceae, or brown algae, evolved later, see page 18). Each of the red and green lineages then diversified further into the various red and green orders and genera that we see today. There is no known fossil record of these first microalgae, but they would probably have resembled today's phytoplankton and, like them, would have lived in the top 330 ft (100 m) or so of the ocean's surface.

**RIGHT** | An electron microscope image through a eukaryotic algal cell, showing the various compartments inside the cell. This cell is from the freshwater species *Chlamydomonas* and is about 10 micrometers wide.

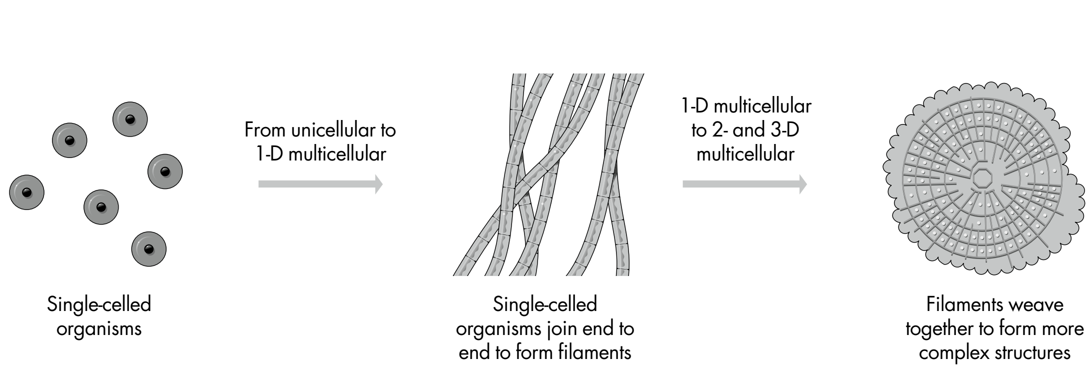
# MULTICELLULAR LIFE FORMS

By around 1.1 GYA Earth's oceans were teeming with red and green unicellular eukaryotic life: the microalgal phytoplankton. The continents that had formed perhaps 3 GYA in the late Archean eon had been weathering for almost two billion years and the runoff was accumulating in the oceans to make them salty. It is just after this point, at around 1.03 GYA, that seaweeds first appear in the fossil record. Seaweeds are simply algae that are made up of lots of cells, rather than one cell. They are multicellular, rather than unicellular, and are called the macroalgae to distinguish them from their unicellular microalgal relatives.

Several evolutionary lineages have independently made this jump from one cell to many, for a range of different reasons. Some organisms, most notably bacteria, can switch between unicellular and multicellular assemblages: when bacterial densities grow too high and nutrients become limited, many bacteria will release chemical signals to indicate that they are beginning to starve. If enough of the bacteria in a population are releasing these signals, then the bacteria flip a series of molecular switches and secrete extracellular polymeric substances—put simply, molecular glue. The bacteria aggregate and become bound together by this glue to form bacterial mats, or biofilms. Biofilms made by marine microbial species can grow one on top of the other, rather like a stack of pancakes, to form large and resilient structures called stromatolites. Fossil stromatolites date back to around 2.8 GYA and bacteria still make them today, although they are hard to find: the best-known stromatolites are from Shark Bay in Western Australia, where each stromatolite stack is about the size of a chair.

Unicellular organisms can also form colonies by joining themselves together in a row, one after the other like beads on a string: we call this a uniseriate architecture. Many bacterial species can be uniseriate, and it is likely that the first seaweeds would have had similar architectures. Such simple filaments are the starting points for more complex structures, all of which we see in modern seaweeds. Filamentous genera, such as the brown *Pylaiella*, form tangles that can be unbranched or branched. Filaments may lose their internal walls and become woven together to form

A POSSIBLE PATH TO MULTICELLULARITY



*Bangiomorpha pubescens*

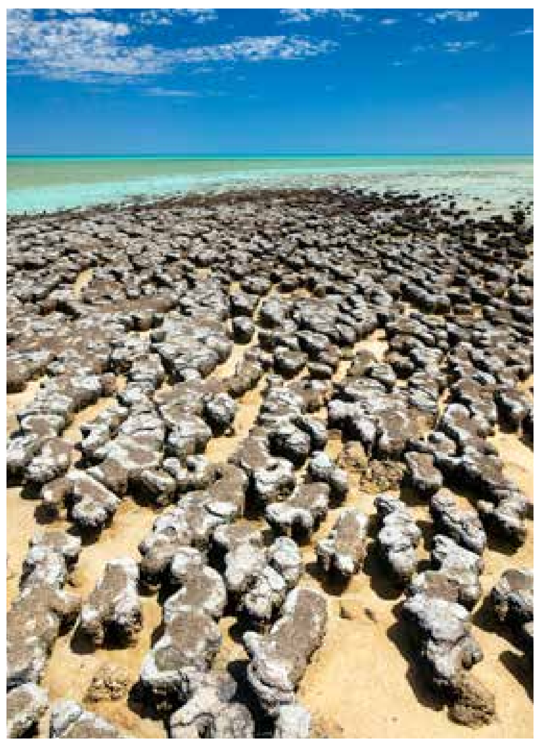
*Proterocladus antiquus*

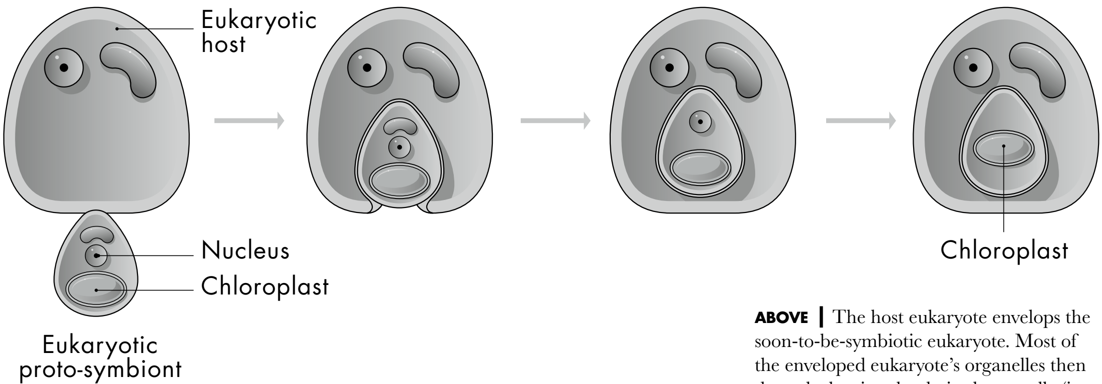
wickerwork-like structures, as in the green *Codium*, or they may divide and spread in two directions rather than one, to give flat sheets, as in the green *Monostroma*, or in three directions, to give the fully three-dimensional kelps.

It is currently thought that simple multicellular filamentous algae, that is true seaweeds, first appeared independently in both the red and green lineages a little over 1 GYA. At the time of writing, the earliest taxonomically resolved multicellular eukaryotic fossil is of a now-extinct red seaweed species called *Bangiomorpha pubescens*, which is around 1.03 GYA. *Bangiomorpha* shows a filamentous branched structure with some differentiation at the tip of the filament into what is presumably a collection of reproductive cells. It is strikingly similar to modern red species such as *Polysiphonia*. The oldest currently known green seaweed is slightly younger, at around 1 GYA, and is of another now-extinct species, *Proterocladus antiquus*. This looked a little like today's green *Cladophora* species, only much smaller at around 2 mm long. The fossil record from a billion years ago is understandably extremely patchy, so these timelines will likely change as further discoveries are made.

**ABOVE** | The 1.03-billion-year-old red seaweed *Bangiomorpha pubescens* is now extinct, but bears a similarity to present-day *Polysiphonia*. Also extinct, the 1-billion-year-old green seaweed *Proterocladus antiquus* bears a similarity to *Cladophora*.

**BELOW** | Cyanobacterial stromatolites in Shark Bay, Western Australia.






**ABOVE |** The host eukaryote envelops the soon-to-be-symbiotic eukaryote. Most of the enveloped eukaryote's organelles then degrade, leaving the desired organelle (in this case, the chloroplast) wrapped in four membranes. For simplicity, the mitochondria are not shown.

## A SECONDARY ENDOSYMBIOSIS

The third lineage of the seaweeds, the Phaeophyceae (brown seaweeds), are only around half the age of the reds and greens, first appearing perhaps 600 MYA (million years ago). They are unusual for two reasons: first, they evolved from a completely separate eukaryotic lineage to the reds and greens and second, they gained their chloroplasts not from a primary, but from one or more "secondary" endosymbioses. That is to say, the proto-brown host engulfed something that had itself engulfed something previously free-living.

The proto-brown host came from a group that evolved into what is commonly called the supergroup Stramenopila. Eukaryotic life is usually classified into around half a dozen major groups. It is generally agreed that animals and fungi sit in one of these major groups, called the Opisthokonts. The brown algal-containing Stramenopila is another of these major groups and the green and red algae sit in a third, called the Plantae (along with the land plants). The rest of the major groups, the Rhizaria, the Amoebozoa, the Excavata, contain various common, but microscopic, amoeba-like organisms. The Stramenopila, therefore, were originally about as different from the red and green algae as humans are.

The proto endosymbionts, on the other hand, are thought to have been red algae. The exact details of the process are the subject of current research, but it is thought that the proto-brown host engulfed one or more red algae around 600 MYA and retained the chloroplasts, giving it the ability to photosynthesize and setting it on the path to a sedentary photoautotrophic lifestyle.

While primary endosymbiosis leaves its resulting organelles wrapped in two membranes, secondary endosymbiosis leaves its resulting organelles wrapped in four. The two inner ones are those that surrounded the original red algal chloroplast, a third is derived from the red alga's cell membrane (the rest of the alga is discarded because the important bit is the chloroplast), and the final, outer, membrane is the remains of the brown host's engulfing cell membrane.

## INVASION OF THE LAND

As always, exact dates are hard to estimate with any confidence, but around 900 MYA, the green algae separated into two groups that are today called the chlorophytes and the streptophytes. Branches in both groups turned from plankton into weeds at various points over the next few hundred million years. However, an important distinction had arisen by the Cryogenian-Ediacaran periods (around 720–540 MYA): while most chlorophyte algae remained marine, the streptophyte algae were beginning to adapt to the waters found inshore near river estuaries.

By this time, billions of years of weathering had turned the river estuaries of the Neoproterozoic (around 1,000–541 MYA) into rich sources of the minerals and elements needed for plant growth. Slowly, but inexorably, one branch of the streptophyte seaweeds moved closer and closer inshore. The more they became adapted to freshwater, the farther they were able to penetrate up rivers. They ran the risk, of course, of being washed up on the banks of those rivers but they began to evolve waxy, protective coats that would protect them from occasional desiccation. In fact, those individuals that were washed up found that the wetlands and riverbanks were extremely nutrient rich and natural selection began to favor those who could hold themselves in place with simple rootlike structures. They began, in short, to evolve into the land plants, making their earliest moves toward the early Ordovician period, perhaps 470 MYA, and starting the plant colonization of the land that built over the next 50 million years or so, through the Silurian period (440–420 MYA) to the early Devonian (around 415 MYA). So, not only were seaweeds the first multicellular organisms to persist on our planet, they also gave rise to the land plants that now support humanity.

# TAXONOMIC VARIATION

In summary, there are three major groups of seaweeds: the reds, the greens, and the browns. The reds and greens evolved as single-celled organisms around 2 GYA. Some members of the greens and reds stayed unicellular and are now phytoplankton, but some branches of both the red and green algae became multicellular and are now the red and green seaweeds. More recently, and perhaps 600 MYA, eukaryotic Stramenopiles engulfed unicellular reds to give rise to the brown algal lineage. As with the greens and reds, some members of the browns remained unicellular and are now phytoplankton (e.g. the diatoms), while other members became multicellular to give rise to the brown seaweeds. In evolutionary jargon, the seaweeds are joined together horizontally, by endosymbiotic gene transfer from one lineage to another, rather than vertically, which would have involved gene transfer from parents to offspring.

Despite being from very distinct evolutionary lineages, all seaweeds have chloroplasts, so all have adopted the same essentially sessile photosynthetic lifestyle and body shapes, but it has either been billions of years since they were the same (reds vs greens) or they were very different to begin with (browns vs greens and reds) and those differences persist today in the fundamental structure and chemistry of each seaweed group.

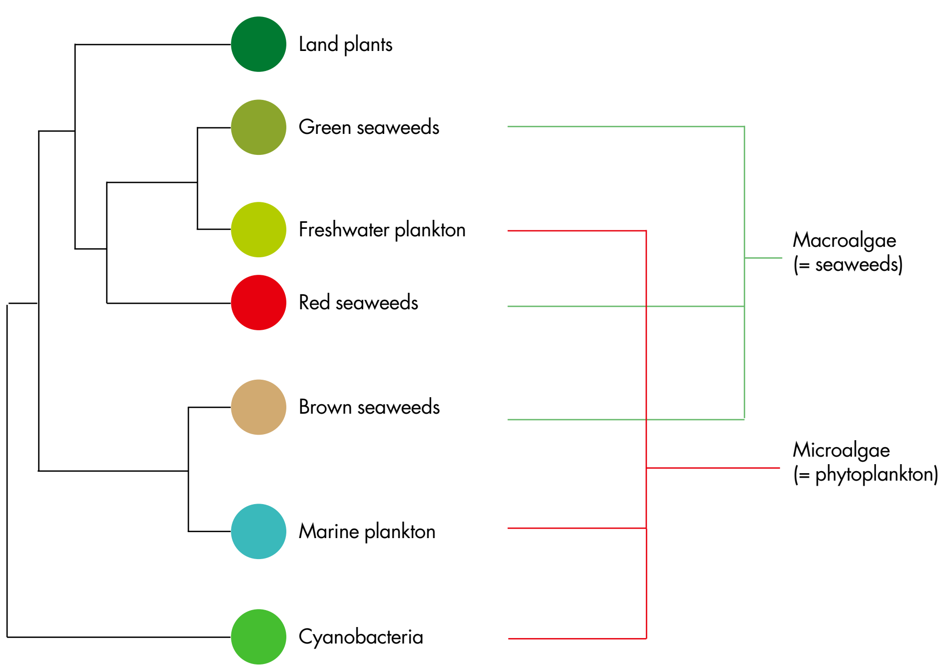
For that reason, the red, green, and brown seaweeds have major differences in their

**BELOW** | A salad of green, red, and brown seaweeds, washed up on a pebbly shore.

biochemical and ultrastructural building blocks. Biochemically, the different lineages have evolved different pigments, which explains their different colors and gives each group its name. These pigments help to absorb light for photosynthesis (see page 38). The different seaweed lineages are also physically constructed from different cell wall polymers. All three of the main seaweed groups have cell walls made of cellulose, which they inherited from their cyanobacterial endosymbionts, but the cellulose fibers are glued together by different branched polymers in each of the three groups. In the green algae, some of these are called ulvans; in the reds, some are the carrageenans and agars; and in the browns, some are the fucoidans and alginates. As we will see, the different chemistry of these polymers means that different groups of seaweeds are suited to different uses. Finally, the red, green, and brown seaweeds have different ultrastructures—that is, the internal structure of the cell. We will not go into too much detail about these ultrastructural differences, although we have already met one: red and green algae have two membranes around their chloroplasts, because those chloroplasts were derived from a primary endosymbiosis, while brown algae have four membranes around theirs, because brown chloroplasts were derived from a secondary endosymbiosis.

**BELOW** | The algal branches of the tree of life. The seaweeds are not as closely related to each other as we sometimes think.

ALGAL TREE



# INDEX